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Normal and abnormal Nests of *Eumenes emarginatus conoideus* (Gmelin) including Notes on Crépissage in this and other members of the genus (Vespoidea, Hymenoptera)

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(*With three plates*)

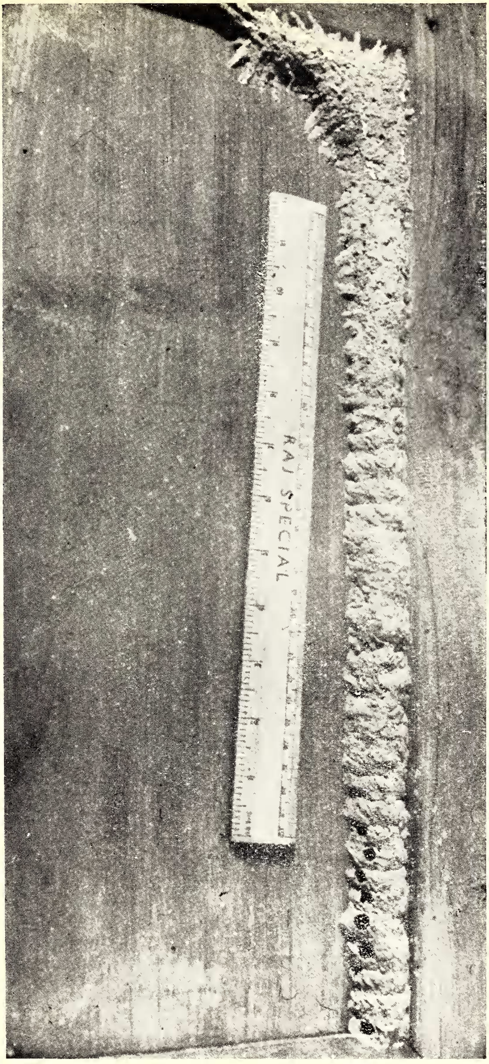
Eumenes emarginatus conoideus (Gmelin) is a fairly common domestic wasp in Bhubaneswar, and all nests here described of this and other species were built indoors, or in roofed-over parts of recent concrete buildings.

Maxwell-Lefroy (1909) and Dutt (1913), who were colleagues and worked on the same material, have written on the biology of *E. e. conoideus* which, following Bingham (1897), they called *E. conica* Fabricius. Iwata (1964), in his recent notes on this subspecies from Thailand, quotes and confirms these authors that its maximum nest-size is 10 cells.

The Table on p. 199 gives data concerning the 12 wasps of this subspecies which we have observed between 23/viii/62 and 9/x/64. Wasps are labelled with *c* followed by a so-called Arabic (or international) numeral; cells within a nest with Roman numerals. Two females (*c*6 and *c*10) were observed during the process of deserting one aggregate of cells and selecting the site for a second, which is designated by the same wasp number followed by a prime (e.g. 6′). Considering wasps *c*2—*c*12 (*c*1 being interrupted) and the thirteen nests they constructed, only three (5, 6, and 10) were completed in the sense that not only was no cell left unfinished or open, but at least the later cells were covered with the granular daubing to which we wish to restrict Roubaud's (1916) term *crépissage* [Jayakar & Spurway, in press, to which we refer for elaboration of our references to *E. campaniformis esuriens* (Fabricius)]. The mothers of two of these nests confirmed their completeness by immediately selecting a second site and beginning a new construct within 2½ hours of finishing the crépissage.

Nest 9 was built on a white-washed wall and round the edge of a cylindrical wooden base for a latch-type door stop. This was 7.5 cm. in diameter, and the first 12 cells of the nest extended upwards round half of its circumference. The remaining 9 were laid down in 3 rows entirely on the wall above the wooden fitment. The giant first nest of *c*10 is shown in Plate II. Cells I to XLI were very standardized in size and shape, though wasps of both sexes emerged from them. They were built one above the other on a wooden shutter in the angle between convex edges of the frame and the flat panel. The mother was marked with paint during the construction of cell XX. The remaining five cells, which were unusually long and narrow, were fitted in somewhat irregularly in the upper corner. The first 3 cells of nest 11 were also partly on a wooden fitment and partly on the vertical wall to which it was attached. The remaining 26 were built entirely on the surface of the wall above it, the mother being painted during the construction of cell XV. These three nests show that a maximum of ten cells is not characteristic of the species at least in this part of its range.

We think it coincidental that both the second nests 6′ and 10′ were the only ones we found built on cane. The cane on which 6′ was built was about 14 mm. in diameter, so 6′ like 6 consisted of the half pots characteristic of the species. However 10′ was built on a partially burnt area of a waste paper basket woven of vertically round canes 5 mm. in diameter and horizontal ribbons. The first cell of 10′ was a complete pot. This was begun, as is usual, as a pair of brackets which were smoothed out and thickened inwards until they were joined to make a floor which was not quite complete, but its outer surface was moulded into the basket work [compare Olberg 1959, p. 122, upper left, for similar work by *E. pedunculatus* (Panzer)]. Thus, one marked individual (*c*10) was seen to construct both complete and half pots, and *E. e. conoideus* must be added to the list of species which are known to have this architectural versatility. The five later pots had similar floors where these were supported by the basket-work, but they were incomplete as they were built overlapping at least one earlier cell. Wasp *c*10 was also seen to twice revisit her first nest after she had built on her second site. The first of these visits was on 21/viii, 5 hours after she deserted nest 10, while she was building cell 10′ II, but the second was five days later (26/viii). On this second visit, however, she did not land, but only



First nest of *Eumenes emarginatus conoideus* 10. 26/viii/64; after emergence had begun.

(*Photo : Dr. J. M. Poehlman*)

Nest of *Eumenes emarginatus conoideus* 12. 13/ix/64. No further loads were brought. The nest is 10–11 cm. high.

(*Photo : Prof. T. A. Davis*)

hovered over nest 10 before flying straight to nest 10′ on what was apparently an inspection visit first thing in the morning. As this was the last day she was seen, this visit to nest 10 might have been pathological, e.g. due to senility. On nest 10′, she put down several daubs before completing cell 10′ VI which had been left unfinished due to sudden rain the night before. She was not seen after the oviposition made on the completion of 10′ VI. The presence of the egg was checked. A wasp visited nest *c*7 on 1/iv which, in the light of the behaviour of the marked *c*10, was probably the mother. Iwata's (1964, p. 334) observation that a wasp was ' plastering a mud coat over the entire surface ' of a 3-celled nest in which all the larvae were already pre-pupae in cocoons suggests that *E. e. conoideus* wasps may sometimes even return to work on their earlier nests.

Female *c*10 thus laid 52 (46+6) eggs to our certain knowledge, for there is no suggestion of any pathological behaviour concerning the exceptionally rapid construction of her first nest. Dr. Iwata (personal communication) tells us that this may be the record number laid by a solitary wasp, and suggests that tropical species have a greater fecundity than their better known temperate relatives (Iwata 1942). If this is confirmed, these nest-building wasps thus differ from birds in whom clutch size increases with latitude.

The range of work speeds was striking. Though most wasps averaged about one cell built, laid in, provisioned, and sealed a day, *c*10 rose to an average of 1·84 and *c* 6 sank to 0·42, *but* for both wasps the exceptional speeds were for only *one* of the two constructs which we saw them build. Wasp *c*6, when building nest 6′, frequently missed a day without bringing a load, and once two days. These absences always left a cell half built, or incompletely provisioned. They were not due to inclement weather and during them she did not return to her already crépissaged first nest.

Crépissage has not, to our knowledge, previously been described in detail for *E. e. conoideus*. This, in wasps of the genus *Eumenes*, consists of finishing off a group of cells by completely covering them with discretely applied lumps of mud so that the construct is left with the appearance of a minute recent mountain chain, whose subsidiary ranges of peaks extend from the cells to the substrate on which these were constructed. As the loads of mud are not worked together as they are put down, the texture remains granular. Though such a structure must be porous, we have once seen a *conoideus* build a vault under her crépissage as is usually done by *E. c. esuriens*. Iwata (1942) considers these vaults to be air-spaces which buffer the cells against temperature changes. We consider that they may also provide protection from parasites such as chrysid cuckoo-wasps who bore into the walls of sealed cells to oviposit. We have seen both *conoideus* and *esuriens* leave the earlier cells naked in large nests, e. g. *c*10 (Plate II). Finally, the crépissage of *esuriens* is made exclusively with the same mud as that with which she builds her cells, in this region red and lateritic. However, all the crépissages we have seen by *conoideus* have been finished-off with some loads of sandy soil so laid down on the ridges, that, by simulating snow, they increase the resemblance to mountains. In the only crépissage we have seen constructed by an *E. pyriformis pyriformis* (Fabricius), ash and cinder dust was used for this finishing (Plate I).

Returning to the Table on p. 199 we note that though several wasps built unexpectedly large nests, two, *c*2 and *c*4, were deserted before even one cell was properly sealed, and two more nests (*c*3 and *c*8) were small. Two of these nests also involved disturbances of the normal sequence. Wasp *c*4, who provisioned but did not seal the only cell she built, put down five loads constructing five abortive brackets at four other sites before adding to the single bracket she had made on the site that had been her first choice. Such intention movements before beginning nest building, which we have also seen made by *E. c. esuriens*, may be no more pathological than they are in birds, but that *c*3 provisioned and sealed her cell I without oviposition is surely a miscarrying of the sequence.

More bizarre is the history of nest 12 (Plate III). This nest was built on the frame and jamb of a window above the stop of the shutter that was the pair of that on which nest 10 had been started exactly six weeks before. It is possible, as the species is not very common, and perhaps likely, that *c*12 was the daughter of *c*10. One abortive bracket of probably two loads was made outside the area photographed. Cell I was small and was left without a lid or an egg overnight. A lip is not an essential feature of a *conoideus* pot and was often omitted by *c*10. However, it was possible that for wasp 12 cell I was unfinished as she did not lay in it. Next morning she first confirmed this interpretation by constructing a lip, however she immediately confounded it by continuing working, putting at least 5 loads on this lip (she was not watched continuously) enlarging it into a little tube which she reinforced on the outside. She spread out the end of this funnel into a lip and sealed the opening with a little knob. Thus cell I had both an abnormal form and was sealed empty. She immediately built cell II, above cell I, continued work on the lip until it was a funnel, and then spent four minutes approaching her abdomen to its mouth and removing it without actually inserting it. It was then realized that she had previously made similar but more trivial abortive egg-laying movements while building both funnels. Her movements suggested that she had not received the proper stimulus to oviposit, not that she was egg-bound. Her behaviour is in contrast to that we have described in an *E. c. esuriens* individual, *e*5, who on several occasions first thing in the morning during provisioning laid an egg. These took a long time and sometimes seemed to necessitate a struggle. These exceptional ovipositions were, we think, stimulated by some change in the egg laid on the completion of the cell. Wasp *c*12 extended the mouth of II into a tube 1·7 cm. long which curved downwards and without sealing this she began cell III. She worked on this and the tube alternately until the cell was complete and fairly normal, and the tube 2·5 cm. long, and the awkward way it curved downwards resembled pictures of the temporary flight tubes constructed by *Oplomerus spinipes* (Linnaeus) [compare Plate III with Olberg (1959) pp. 140-149].

Next day, *c*12 pathologically added to lip III, and built IV including excrescences which were later added to and became the first two brackets of V. This may not itself be pathological but merely a consequence of the cells being distorted in shape ; *c*10, when fitting the later cells of her great nest into the corner of the shutter, often left well-worked ridges which she later extended, often with gross modification, to become the brackets of the next, or even later, cells. *c*12 was next etherised and painted, and did not return that day. Next morning she thickened lip IV and continued building V above it. Again she made what later was used as the first bracket of VI, but succeeded in ovipositing in V.

Though this, her first egg, was present at 13·05, she did not bring her first prey until next day when she inserted the bluish green semi-looper Noctuid larvae which were the prey used, apparently exclusively, by *c*10, *c*11, and *c*12. Unfortunately she put larvae into the egg-less cells III and IV as well as in V, and then sealed the egg-less IV only. She then built VI so that its walls enclosed the open mouth of V, from which a prey walked out into the unfinished cell and was collected by the observers.

Next day, she apparently pushed another larva back into V before it had completely escaped, and continued cell VI, finished it, and oviposited. The cavities of cells V and VI were thus continuous. She provisioned cell VI apparently normally, sealed it and built cell VII. She then drew her abdomen up to the lip and relaxed it repeatedly for over a minute. After this frustration, she extended the lip for 1 cm. without curving it in any way. The mud work of this tube was exceptionally coarse and the loads were extended on to the cell walls of VII. She immediately laid an egg in the mouth of tube VII, doubtless as deep as she could reach with her abdomen.

Not till next day did she try to insert prey into this tube. This prey both dislodged the egg and itself lodged in the tube.

She sealed VII and built VIII, again above it, oviposited, and provisioned. She may have had trouble with her prey and was once seen standing on her hind legs on tube II while maxillating a caterpillar. There is a distinct suggestion in our notes that either *c*12 did not render her prey as passive as other wasps, or more likely they could not be inserted so deftly into these cells which were more abnormally shaped than has been emphasised, but which is well shown in Plate III. Cell VIII was sealed by the end of the day. Next day she built IX above VIII, laid, and put in at least one larva. A chrysid was then seen on the nest. *c*12 then put down a few daubs and began crépissage. She also dropped at least one load, and took away another not putting it down. A chrysid made another visit, and then two more loads were added to the crépissage. Next morning she made at least two loadless visits, on the second of which she was followed by a sarcophagine fly who, when the wasp had left, oviposited or larviposited in IX. A chrysid again arrived, four minutes later *c*12 arrived, and immediately left the nest, and for the next 16 minutes hovered over similar furnishings on the verandah, never returning to the construct. She thus made a definitive desertion due to parasitization. Next morning ants removed the prey from III and a spider was captured carrying an apodous larva, perhaps of one of the parasites. A wasp emerged, apparently from VII, not from VIII which was the only normally filled cell. As has been noted, all the cells were contorted in shape.

Roubaud (1916) had discussed such dysgenic sequences of behaviour in the African *E. tinctor* Christ, and interpreted them as responses to the frustrations due to suboptimal microclimates, either seasonal or geographical. We have discussed elsewhere Roubaud's examples and those we have observed in *E. c. esuriens.* Such behaviour seems much more frequent in *conoideus* than in the commoner *esuriens* in this locality; however, we have yet to see one female *esuriens* making two constructs or any containing more than thirteen cells. This supports Roubaud by suggesting that *conoideus* is in some way at the edge of its ecological range, where, as would be expected on some theories of population expansion, some individuals, perhaps genetically exceptional, do exceptionally well, while other individuals are exposed to strains to which they are unequal.

However, *c*12 seemed to suffer from an internal insufficiency so that, though not egg-bound, she only made low intensity attempts to oviposit at the appropriate time in the cycle. Whether or not this was in some way due to the environment (e.g. through nutritional inadequacy) is irrelevant to the demonstrations it gave of the role played by such actions in a cycle of instinctive activities. Oviposition, perhaps because the wasp reacts to the presence of an egg, or because the action of laying provides Sherringtonian proprioceptive consummatory stimuli, inhibits one phase of the cycle (in this example mud working), and therefore permits the initiation of the next phase (in this example provisioning). However, the behaviour of *c*3 did not conform to this Lorenz-Tinbergen instinct theory analysis. After she had failed to lay in cell I she pro-